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A CRITICISM OF THE EVIDENCE FOR THE MUTATION THEORY OF DE VRIES FROM THE BEHAVIOR OF SPECIES OF OENOTHERA IN CROSSES AND IN SELFED LINES

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The mutation theory of Professor De Vries rests so very largely upon deductions from his studies on species of Oenothera that any discussion of it naturally centers upon the interpretation of the behavior of these plants when selfed (in-bred) and in their crosses with one another. Of these species *Oenothera Lamarckiana* stands as the form most thoroughly studied with respect to its habit of throwing off in successive generations variants with numerous distinguishing characters of such a nature that they can with certainty be separated and would rank in systematic botany as clearly defined new species arising suddenly and fully formed from the parent type. Professor De Vries calls these variants 'mutants' and interprets their appearance as the spontaneous origin by mutation of new species from a plant, *Oenothera Lamarckiana*, which he believes to be representative of a pure species. De Vries is not willing to allow that in *O. Lamarckiana* this phenomenon may be the direct result of an impure or hybrid constitution. The behavior of *O. Lamarckiana* and certain other forms in this genus is, therefore, to De Vries direct experimental evidence of the origin of new species through wide and discontinuous variations, the result of spontaneous internal manifestations within the parent plants. De Vries further believes that mutations play a very important part in organic evolution and that they largely supply the material, i.e., the variations, upon which natural selection can operate.

There is no question of the facts as brought out in the extensive and patient work of De Vries; they have been repeatedly confirmed. *Oenothera Lamarckiana* if grown in sufficiently large cultures may be expected to produce in each generation approximately the same set of 'mutants.' The proportions differ but they are apparently fairly stable for each variant; some make up about 1–2 per cent of the cultures, others are much less common. Certain of the 'mutants' breed fairly true when selfed while some are more unstable than the parent *Lamarckiana*. A significant feature of this performance is the clear expression of order and system in the appearance of precisely the same types through successive generations and we have no reason to suppose that *O. Lamarck-*

iana is likely to give up this habit of throwing variants however long it may be cultivated.

Now the regularity with which *Oenothera Lamarckiana* produces its 'mutants' through successive generations indicates conditions within the germ plasm of such a nature that a number of different specific types of sexual cells are produced rather than a single set of gametes uniform in their germinal constitution. There is really not the spontaneity in the production of new forms by *Lamarckiana* which one might expect of a plant in a state of 'mutation' with an organization expressing itself in irregular and unexpected departures from the type through peculiarities of mutating instability in its germinal constitution. Consequently a critic of the evidence for the mutation theory offered by De Vries from the behavior of *Lamarckiana* very naturally is led to question the fitness of this plant as representative of a pure species. The discussion must finally center on the problem of whether or not the germinal constitution of *O. Lamarckiana* is homozygous, i.e., carrying two identical sets of hereditary factors derived from the parents through each sexual union. May not the germinal constitution be heterozygous, or hybrid, the two sets of hereditary factors in some respects differing from one another?

An organism homozygous in germinal constitution can develop only one type of sexual cells, gametes, and these will be identical with those of the parents unless chemical or physical conditions affecting the germ plasm modify directly the germinal constitution carried through the succession of cell divisions that make up a generation, or upset the precision of the reduction divisions previous to the formation of gametes, or acting directly on the gametes themselves change their organization. Variations of the germinal constitution introduced in this manner would constitute mutations and it is an admitted fact that variations which might be interpreted as mutations are very rare in the lines of animals and plants which are believed to be most pure and are consequently most stable in their breeding behavior.

A heterozygous organism must at the time of gametogenesis distribute the hereditary factors unevenly whenever these factors as they come from the two parental lines differ from one another. There are many reasons why hereditary factors are believed to be present in the chromosomes, and the reduction divisions which distribute whole chromosomes into two group clearly furnish a mechanism by which a segregation of factors may take place. The most complete and satisfactory studies on chromosome reduction for both animals and plants have

established the fact that the two sets of chromosomes, derived one from each parent, constitute two series of homologous pairs and that the members of these pairs become closely associated before the reduction divisions and are later separated by this mitosis which may properly be termed a segregation division.

Studies on the reduction divisions of *O. Lamarckiana* and some of its derivatives by Geerts, Gates, Stomps, Lutz and Davis have shown loose associations such that the mechanical conditions favor irregularities of distribution which actually do occur and gametes are known to be sometimes formed with one more or one less chromosome than 7 which is the normal number for the genus. In the two 'mutants' *lata* and *scintillans* there have been observed 15 chromosomes, obviously the result of the union of gametes bearing unlike numbers of chromosomes. Forms with 21 chromosomes are also known which apparently arise from the fertilization of an unreduced egg (14 chromosomes) by a normal sperm nucleus (7 chromosomes). There is also a very rare type, *gigas*, with 28 chromosomes which has been matched in chromosome number by analogous forms discovered by Bartlett from other species of Oenothera. This irregular behavior of the chromosomes in *Lamarckiana* and its 'mutants' gives strong cytological evidence of conditions such as might be expected in heterozygous material where the two sets of chromosomes from parental lines are dissimilar in their genetical constitution and consequently fail to pair closely previous to segregation through the reduction division. One of the oenotheras, a race of *grandiflora*, has been found to present an orderly assembling of chromosomes in pairs at the time of reduction together with an equal distribution of the members of each pair and this history in one of the more stable forms serves to emphasize the striking irregularities of *Lamarckiana*. Therefore the cytological evidence is distinctly favorable to a view that *Oenothera Lamarckiana* contains a chromosomal complex of a mixed or hybrid character rather than two similar sets of chromosomes.

On the genetical side there is more obvious evidence of the heterozygous nature of *Oenothera Lamarckiana*. It is a law of genetics that crosses between organisms which produce uniform gametes must give uniform progenies in the first generation and this constitutes a reliable test of whether or not the parents are monogametic; if the first hybrid generation contains distinct classes then one or the other or both of the parents must have produced more than one kind of fertile gametes. De Vries discovered the striking fact that when *Lamarckiana* and some of its mutants are crossed with certain wild species of Oenothera their

progeny in the first generation fall into two groups sharply separated from one another and these De Vries termed 'twin hybrids.' Since the twin hybrids are produced in crosses of *Lamarckiana* with several species some of which when crossed among themselves give uniform progeny in the first generation the evidence indicates that *Lamarckiana* must supply the two different types of gametes which make possible this splitting in the first generation. De Vries holds that the cause of twin hybrids lies in the state within the gametes of certain factors called pangens whether active, inactive or labile and this appears to be an admission that *Lamarckiana* does not form equivalent gametes.

Long experience of plant and animal breeders has led them to suspect that pronounced sterility in an organism indicates hybrid constitution and critics of the purity of *Oenothera Lamarckiana* have pressed the point that in this plant approximately one-half of the pollen grains and ovules abort and that the proportions of fertile seed are low, being from about 30 to 40 %.

Extensive studies of Geerts followed by observations of other workers have shown these conditions to be generally characteristic of species of Oenothera and allied genera. These facts indicate the necessity of detailed studies on the cytology of gametogenesis, fertilization and embryo formation. Thus if it could be shown that in every group of four pollen grains, tetrad, formed as the result of the reduction mitoses only two grains are perfect the conclusion would be justified that the pollen sterility was the result of this segregation division. Unfortunately the abortion of pollen grains takes place after the members of the tetrad have separated and the relation of sterile pollen grains to one another and to the perfect grains is not evident, but it is a fact that shriveled, sterile pollen is distributed among the perfect grains so evenly as to suggest an origin through the reduction division rather than from some physiological cause such as malnutrition, which under certain conditions is known to produce high degrees of sterility.

The facts of gametic and zygotic or seed sterility have, however, suggested certain working hypotheses that must be considered in present and future research on oenotheras. Thus it is possible to conceive of impure or heterozygous species capable of reproducing their lines (breeding true) and showing little or none of the phenomenon of hybrid splitting provided only such gametes and seeds are fertile as will reproduce the hybrid type. Renner has applied this line of reasoning to *Lamarckiana* by assuming that the small proportion of fertile seeds of this plant are those formed by the union of the two different types of gametes

which produce the twin hybrids and that homozygous combinations of gametes are represented in the sterile seeds. Occasional fertile combinations of gametes varying from the usual type may then be responsible for the so-called mutants which owe their peculiarities to segregation phenomena, to be expected in a hybrid, rather than to spontaneous modifications such as are assumed by the mutation theory.

Finally, in this brief criticism of *Oenothera Lamarckiana* as representative of a pure species and therefore suitable material for conclusions on the importance and character of mutations in organic evolution it should be pointed out that there is no evidence that this plant is a wild species native to the American continent which was the original habitat of the group. On the contrary we have reason to believe that *Lamarckiana* was brought into cultivation from material growing in England where the early introduction of oenotheras established some extensive colonies probably of mixed and hybridized character. It has also been found possible by crossing two carefully selected species of Oenothera (*franciscana* × *biennis*) to synthesize a hybrid scarcely to be distinguished in its systematic characters from *Lamarckiana* and this product which has been named *neo-Lamarckiana* forms twin hybrids when crossed with certain species that give twin hybrids with *Lamarckiana*. *Neo-Lamarckiana* when selfed throws a much larger progeny of variants than does *Lamarckiana* but this fact seems to be correlated with its much higher seed fertility, from 84 to 87 %. These variants have been repeated in their essential characteristics through three generations and the parallel of this behavior to that of *Lamarckiana* is very close although as would be expected, the types of variants are not the same. Thus an undoubted hybrid among the oenotheras has been shown to present breeding habits similar to those of *Lamarckiana*. The behavior of *neo-Lamarckiana* when selfed appears most readily explained as due to the breaking up of a hybrid rather than by principles of mutation since characters more or less similar to those of the parents appear among the derivatives.

In addition to the studies on *Oenothera Lamarckiana* and its 'mutants' there has been a very large amount of work by De Vries, Gates and others involving other species of Oenothera and more recently extensive studies by Shull, Bartlett and Atkinson. These have brought out some very puzzling situations in the behavior of Oenothera species in crosses. In some cases the first generation hybrids show pronounced resemblance to the paternal parent of the cross, in other cases to the maternal parent, and still other combinations give blends with inter-

mediate characters such as frequently appear in the first generation. Second generations in some cases breed fairly true, in others show extensive and characteristic splitting usual to hybrids. Back crosses in some combinations reproduce almost exactly one of the parent types. Shull in a remarkable series of crosses has obtained in the first generation polymorphic progenies of much greater complexity than the twin hybrids of De Vries. Atkinson has described quadruple hybrids in the first generation from crosses between two wild American species. Bartlett has found that selfed lines of certain American wild species may throw 'mutants' in proportions as high as 50, 80 or even 100 per cent of the cultures.

Explanations of these extraordinary types of behavior are not yet clear. Atkinson, insisting on the purity of the species with which he worked, proposes a view that multiple progenies in the first generation are determined by the selection or differentiation of factors in the fertilized egg or zygote, an hypothesis which will require cytological evidence to be convincing. Bartlett holds the view that different classes of gametes are formed, an attitude in accord with much evidence from various studies on animals and plants. This seems to the writer to be an admission of impurity of germinal constitution unless it be shown that gametes may mutate in immense proportions, a view which has no support from genetical and cytological studies in general. None of these investigators seem inclined to admit the possibility or probability that the complexities of Oenothera genetics may be the result of germinal impurity widespread among the species as the result of extensive hybridization.

Yet the high degrees of gametic and zygotic sterility now known for certain forms of Oenothera makes it possible to conceive these species as impure, maintaining themselves because for the most part only those gametic combinations are fertile which will reproduce the heterozygous condition. Variants in selfed lines from such stock would most naturally be interpreted not as mutations but as the result of other gametic combinations which prove to be fertile. Crosses between impure species are, of course, crosses between hybrids and the behavior of their progeny, especially when high degrees of sterility are present, would naturally be expected to prove unusual and irregular. Only recently has the importance of sterility and delayed seed germination received serious consideration in problems of Oenothera genetics and no investigations have as yet been published which give the matters full consideration.

In conclusion it should be noted that although most of the genetical work on oenotheras has not been interpreted by the Mendelian system of notation there is, nevertheless, clear evidence of order in the sharply defined results of both inbreeding and crossing. A few cases are known of simple and clean cut segregation in ratios fairly close to Mendelian expectations, notably in crosses between *Lamarckiana* and *brevistylis* and probably in time more of these will be found. The difficulty has been to discover and to isolate simple material in the confusion of mixed and impure forms present in this group of plants. A great forward step will be taken in Oenothera genetics when types of proven purity have been established, since such forms as standard material in breeding tests may prove to be the keys that will open doors of mystery.

THE SPECTRA OF ISOTOPES AND THE VIBRATION OF ELECTRONS IN THE ATOM

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According to most of the recent theories of atomic structure and of the origin of light, the emission of light is due to the vibration of the non-nuclear electrons in the atom, but there is a difference of opinion in regard to the process by means of which the radiation takes place. The frequency of the light has usually been assumed to be that of the vibrating electron which emits it, but the theory of Bohr[1] indicates a less simple relationship according to which the frequency of the light varies as the increment of the two-thirds power of the electronic frequency.

The investigation reported in this paper was begun several years ago for the purpose of determining if the electronic periods are wholly dependent upon the *net* positive charge on the nucleus of the atom. In order to get a more definite statement of the problem, it may be assumed that the nucleus of any atom contains a positive electrons and b negative electrons. The net positive charge on the nucleus may be taken as $a - b$ or P. While P is not known exactly it is probably equal to or only slightly greater than the atomic number N. A single element, such as lead, is characterized by a single value of P. Isotopes are different atomic species of the same element, all with the same value of P, but with different values of a and b. Since $a - P = b$, the numerical value b gives not only the number of negative electrons, but also the